MIGRATION AND DISTRIBUTION OF PINK SALMON SPAWNERS IN SASHIN CREEK IN 1965, AND SURVIVAL OF THEIR PROGENY

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ABSTRACT

The escapement of 14,813 pink salmon (*Oncorhynchus gorbuscha*) to Sashin Creek, southeastern Alaska, in 1965, followed by the emergence of 2.2 million fry, or 18 percent of the potential egg deposition, represented a relatively high survival of eggs and alevins in a stream, where the long-term average is 7 percent. This high survival was predicted from an established relation between survival of eggs and alevins and the time the parents entered Sashin Creek to spawn.

The spawning ground was divided into three areas—upper, middle, and lower—to study density of spawners and survival of their progeny. Density in 1965 was higher in the middle and upper areas than in the lower. From egg deposition to fry emergence, survival was estimated to be 23 percent in the upper area, 18 percent in the middle area, and 14 percent in the lower area.

The instantaneous rate of mortality remained relatively unchanged from deposition of eggs to emergence of fry in the upper and middle areas. In the lower area, mortality was relatively high during spawning and low between spawning and hatching of eggs. Much of the mortality throughout the stream was traced to the disappearance of eggs and alevins. Factors causing this disappearance included retention of eggs, superimposition of redds, predation, and turbulent water. A drought during spawning retarded development of embryos and caused considerable mortality.

The numbers of pink salmon (*Oncorhynchus gorbuscha*) fluctuate drastically from year to year, and knowledge of the natural processes that cause the fluctuations is required if the resource is to be managed effectively. To evaluate mortality of pink salmon in fresh water, the Bureau of Commercial Fisheries has studies in Sashin Creek, a small spawning stream on Baranof Island, southeastern Alaska.

Adult pink salmon entering Sashin Creek have been counted each year since 1934, and fry leaving have been counted since 1941. Adults have numbered from 8 to 92,085 and fry from 50 to 5,940,300; fresh-water survival has ranged from 0.06 to 21.75 percent of potential egg deposition (table 1).

Only a small portion of Sashin Creek can be used by salmon spawners. Although the Creek is about 4,000 m. long, a waterfall 1,200 m. from the head of tidewater prevents further upstream movement of fish. Spawning is limited in a narrow canyon that extends 300 m. downstream from the waterfall and in the intertidal zone, where the gradient is steep and the bottom is mostly bedrock. The main spawning ground (13,629 m.^{2}) lies between the intertidal zone and the canyon.

Four factors that affect survival of pink salmon in Sashin Creek have been discussed by Merrell (1962) and McNeil (1966): (1) time of migration of spawners, (2) distribution of spawners, (3) density of spawners, and (4) weather. To clarify further the relation of these and possibly other factors to survival of eggs, alevins, and fry in Sashin Creek, I studied a relatively large run of pink salmon that spawned there in late August and in September 1965. Survival from deposition of eggs to emergence of fry was estimated in three areas that included 97 percent of the total spawning ground used by spawners in years of large escapements.

In this paper, I describe the migration, distribution, and density of pink salmon spawners in the summer of 1965, and the survival of their progeny in fresh water. Also, I discuss: (1) the relation of survival of eggs and alevins to time of spawning of adults, (2) variation among stream areas in density of fry, (3) relation of water quality (primarily concentration of dissolved oxygen) to survival and development of embryos, (4) disappearance of eggs and alevins from spawning beds, and (5) seasonal variation in mortality in spawning beds.

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TABLE 1.—*Number of adult pink salmon in each escapement, potential egg deposition, number of fry produced, and fresh-water survival for brood years 1934–65, Sashin Creek, southeastern Alaska*

Brood year [1]	Adults in escapement	Potential egg deposition [2]	Fry produced	Fresh-water survival
	Number	*Number*	*Number*	*Percent*
1934	7,917	----	----	----
1935	6,323	----	----	----
1936	5,364	----	----	----
1937	9,085	----	----	----
1938	6,467	----	----	----
1939	16,830	----	----	----
1940	53,594	52,858,000	3,399,900	6.43
1941	84,303	88,678,000	1,024,300	1.16
1942	92,085	78,894,000	674,000	0.85
1943	14,883	14,980,000	227,800	1.52
1944	4,050	3,904,000	105,600	2.71
1945	5,465	5,062,000	43,100	.85
1946	933	736,000	1,200	.16
1947	1,486	1,330,000	27,600	2.07
1948	597	516,000	9,100	1.76
1949	4,902	4,800,000	176,200	3.67
1950	112	86,000	50	.06
1951	4,366	4,062,000	412,500	10.15
1952	45	(3)	740	----
1953	1,164	1,284,000	95,400	7.43
1954	21	12,000	660	5.48
1955	9,267	10,286,000	266,200	12.31
1956	933	1,018,000	5,040	.50
1957	2,834	2,588,000	562,900	21.75
1958	217	174,000	10,700	6.13
1959	35,391	40,379,000	5,332,400	13.21
1960	162	(3)	480	----
1961	28,759	29,425,000	5,940,300	20.19
1962	8	8,000	100	1.20
1963	16,757	16,640,000	3,256,300	19.57
1964	[4] 2,193	2,230,000	[5] 310,000	13.91
1965	14,833	12,668,000	[5] 2,235,000	17.92

[1] The term "brood year" refers to the year of spawning.

[2] Based on 2,000 eggs per female except when actual fecundity was calculated in 1942 (1,936 eggs), 1957 (1,988 eggs), 1959 (2,040 eggs), 1960 (1,903 eggs), 1961 (1,991 eggs), 1963 (1,908 eggs), 1964 (1,709 eggs), and 1965 (1,782 eggs).

[3] An attempt was made to destroy the spawners.

[4] Natural escapement (327) was reinforced by introduction of 1,866 adults.

[5] Fry weir was not functioning; estimate based on number of preemerged alevins in spawning beds.

MIGRATION, DISTRIBUTION, AND DENSITY OF SPAWNERS

Fresh-water survival of pink salmon eggs and alevins in Sashin Creek is inversely related to the time of migration of the spawners (Skud, 1958; Merrell, 1962). Because pink salmon are mature when they enter Sashin Creek, early entry into the stream means early spawning and late entry gives late spawning. The date by which 50 percent of all of the spawners had entered the Creek is used in this paper to index the time of spawning. In 1965, 50 percent of the spawners had entered the Creek by August 26, which was the fourth earliest date of record. I had expected, therefore, that survival of the eggs and alevins would be high.

The distribution and density of spawners in 1965 were analyzed to determine if spawners concentrated in areas that afforded the best habitat for embryos and alevins. Ninety-seven percent (13,084 m.^{2}) of the Sashin Creek spawning ground was divided into three areas—upper (2,945 m.^{2}), middle (4,067 m.^{2}), and lower (6,072 m.^{2}). The upper area has a relatively high gradient and coarse materials in the bed; the middle area has an intermediate gradient and medium-sized materials; and the lower area has a low gradient and relatively fine materials (table 2).

TABLE 2.—*Average gradient and size composition of bottom materials* [1] *in three areas in Sashin Creek*

Area	Average gradient	Bottom composed of—		
		Coarse particles [2]	Medium particles [2]	Fine particles [2]
	Percent	*Percent*	*Percent*	*Percent*
Upper	0.7	81	16	3
Middle	.3	61	26	13
Lower	.1	47	36	17

[1] Procedures for sampling bed materials to measure size composition were described by McNeil and Ahnell (1964).

[2] Coarse particles are >12.7 mm. diameter; medium particles are 1.68 to 12.7 mm.; fine particles are <1.68 mm. diameter.

In years before 1965, when spawners were abundant they used the entire Sashin Creek spawning ground but concentrated in the middle area. Nevertheless, the upper area produced more fry per unit area of streambed than the middle or lower area (Merrell, 1962; McNeil, 1966). When spawners were scarce, they usually concentrated in the lower area and did not use the upper area at all. The failure of spawners to use the potentially most productive upper area raises important questions about factors that control their distribution.

In 1965, 14,813 pink salmon spawners, including 7,109 females, entered Sashin Creek. Two hundred of the females were captured as they passed the weir and were tagged with plastic Petersen disks 1.6 cm. in diameter, fastened below the dorsal fin. Fifty fish were tagged with white disks on August 18, 50 with red disks on August 24, 50 with yellow disks on August 28, and 50 with green disks on September 12. The dates of release of the tagged females were selected to ensure representation of the early, middle, and late portions of the migration to fresh water. Seven percent of the total number of females (7,109) had entered Sashin Creek before the first date of tagging (August 18); 37 percent before the second date (August 24); 70 percent before the third date (August 28); and 95 percent before the fourth date (September 12). An observer on foot counted tagged and untagged females in each area and recorded their location. Only females were counted because they determine potential egg deposition.

The females were easy to count on the spawning ground because they remained near the site of their redds from the beginning of spawning until they died. I evaluated this behavior, which is typical of spawning females, by observing 14 tagged females that were spawning in a 100-m.-long section of Sashin Creek. The locations of the 14 females were determined twice daily with a transit and stadia and were plotted on a detailed map. The average longevity on the spawning ground of the 14 females was 11.5 days (range 3 to 20 days). The average size of the area occupied was 3.8 m.^{2} (1.4 m. wide by 2.7 m. long). The smallest area occupied, 0.6 m.^{2}, was for a fish that lived only 3 days after establishing a site, and the largest, 17.3 m.^{2}, was for a fish that lived 9 days. All died near their redds.

One method of estimating the number of females that spawned in an area was to sum the daily counts of untagged females and divide by their average longevity. The daily counts were summed by fitting a curve to the number of untagged females counted each day and measuring the area under the curve (examples are given by McNeil, 1964a and 1964b). Average longevity was estimated from daily observations of tagged females. One day was added to the number of days individual tagged females were observed because I assumed they occupied the spawning ground one-half day before they were first observed and one-half day after they were last observed.

Estimates of the number of females in each area based on summed daily counts and average longevity were 2,040 in the upper area, 3,095 in the middle, and 3,051 in the lower. I assumed that 97 percent of the total number of females spawned in the three areas, and my estimate for the whole stream was 8,439 females, or 118.7 percent of the number counted at the weir. The estimates for each area were, therefore, adjusted by dividing by 1.187. The resulting estimates were 1,719 females in the upper area, 2,607 in the middle, and 2,570 in the lower.

A second method of estimating the number of females in each area was based on the occurrence of tagged females. I assumed that tagged and untagged females were distributed similarly. Of the

TABLE 3.—*Density of female pink salmon spawning in three areas of Sashin Creek, based on observations of untagged females (summed daily counts) and tagged females*

Area	Females per square meter, based on—		Mean of the two estimates
	Observations of untagged females	Observations of tagged females	
	Number	*Number*	*Number*
Upper	0.58	0.57	0.58
Middle	.64	.59	.62
Lower	.42	.46	.44

200 tagged females released, 184 (92 percent)[1] were recorded in the study areas: 45 in the upper area, 64 in the middle, and 75 in the lower. On the further assumption that 97 percent of the females counted at the weir spawned in the three areas and were distributed in the same proportion as the 184 tagged females, I estimated that 1,689 females spawned in the upper area, 2,399 in the middle, and 2,813 in the lower.

The density of females spawning in each area was calculated by dividing the total number of females by the area of spawning bed. The estimates of density of females in each area by each of the two methods for estimating the number of females agreed closely (table 3) and indicated that density of spawners was about the same in all areas. Although the observed number of tagged females in each area was not significantly different from the expected number calculated from an assumed uniform density of tagged females (table 4), the conclusion that the average density of females was identical among the areas is less attractive than the conclusion that small differences existed. I will use, therefore, the mean of the two estimates of density for each area (table 3) as the best (most probable) estimate of density in my calculations of potential egg deposition.

[1] Additional tagged females may have spawned in the study areas but were not seen.

TABLE 4.—*Numbers of tagged female pink salmon observed in three areas in Sashin Creek and the expected number, based on an assumed equal density*

Area	Female pink salmon	
	Observed	Expected
	Number	*Number*
Upper	45	41.4
Middle	64	57.2
Lower	75	85.4

x^2 (2 d.f.) = 2.39 (P, 0.30).

SURVIVAL OF EGGS AND ALEVINS

Estimates of survival of eggs and alevins in this paper pertain to three periods in the fresh-water life of 1965 brood year pink salmon:

Period	*Months*
1. Egg deposition (late August through September)	1.3
2. Egg deposition and hatching (October through mid-November)	1.7
3. Hatching and fry emergence (late November into late March)	4.2
Total	7.2

Survival in the nth period is calculated by:

$$S_1 \cdot S_2 \quad \cdot \quad \cdot \quad \cdot \quad S_n = S \qquad (1)$$

$$S_n = \frac{S}{S_1 \cdot S_2 \cdot \cdot \cdot S_{(n-1)}} \qquad (2)$$

The symbol S is total survival from beginning of spawning to any selected date, and an estimate of S ($\hat{S}$) must account for dead eggs and alevins that may have disappeared from the population before the date of sampling. The estimate must also give a value $\hat{S} \leq 1.0$. To satisfy these requirements, the estimate of survival is calculated from:

$$\hat{S}_j = \frac{\frac{1}{k}\sum_{i=1}^{k} T_{ij}}{e_j} \cdot \frac{\sum_{i=1}^{k} a_{ij}}{\sum_{i=1}^{k} T_{ij}} \qquad (3)$$

with the condition that

$$\frac{\frac{1}{k}\sum_{i=1}^{k} T_{ij}}{e_j} \leq 1.0 \qquad (4)$$

In equations (3) and (4),

i designates an individual sampling ($i=1$ to k),
j designates an individual area ($j=1$ to 3),
a_{ij} is the number of live eggs and alevins collected at the ith point of the jth area,
T_{ij} is the total number of eggs and alevins (live and dead) collected at the ith point of the jth area,
e_j is the average potential egg deposition in the jth area, and
$\hat{S}_j$ is an estimate of S for the jth area.

For the case where

$$\frac{\frac{1}{k}\sum_{i=1}^{k} T_{ij}}{e_j} < 1.0$$

equation (3) reduces to

$$\hat{S}_j = \frac{\frac{1}{k}\sum_{i=1}^{k} a_{ij}}{e_j} \qquad (5)$$

I used equation (5) in an earlier paper (McNeil, 1966) to estimate survival of pink salmon in Sashin Creek.

The average density of eggs and alevins was estimated in each area from samples obtained with hydraulic sampling equipment described by McNeil (1964a). The points sampled, each representing 0.1 m.^{2} of the streambed, were selected randomly within the three study areas with the aid of tables of random numbers. Eggs were collected after spawning (September 29), and eggs and alevins were collected during hatching (November 20) and before emergence (March 26).

In calculating $\hat{S}_1$ (equation 3 or 5), I assumed that the number of eggs collected at each point was 93 percent of the number actually present at the time of sampling (McNeil, 1964a). Potential egg deposition was calculated by multiplying the average fecundity by the estimated average number of females that had spawned per square meter (table 3). The average fecundity, based on 20 randomly selected unspawned females taken at the weir on the four dates females were tagged, was estimated to be 1,782 eggs.

Estimates of survival from August 20 (beginning of spawning) to September 29, November 20, and March 26 are given for each area in table 5. These estimates were calculated directly from equation (3).

The estimated number of eggs per square meter in the middle area at the end of spawning was greater than the estimated potential egg deposition (table 5). Two sources of error could have contributed to this discrepancy: (1) Potential egg deposition may have been underestimated, or (2) the number of eggs at the end of spawning may have been overestimated.

The use of an area by spawning salmon can be indexed in two ways—directly by observing the density of spawners (table 3) and indirectly by

TABLE 5.—*Potential egg deposition, number of live and dead eggs and alevins, ratio of live to combined live and dead eggs and alevins, and survival of 1965 brood pink salmon in three areas of Sashin Creek*

Area	Potential egg deposition per square meter		Period beginning August 20 and ending—	Eggs and alevins per square meter				Calculated survival
				Combined live and dead		Ratio of live to combined live and dead		
	Mean	90-percent confidence limits of mean		Mean	90-percent confidence limits of mean	Mean	90-percent confidence limits of mean	
	Number	*Number*		*Number*	*Number*	*Percent*	*Percent*	*Percent*
Upper	1,034	±72	September 29	966	±216	84	±5	78
			November 20	711	±191	86	±5	59
			March 26	433	±153	54	±16	23
Middle	1,105	±77	September 29	1,504	±312	86	±4	[1] 86
			November 20	765	±222	80	±8	55
			March 26	428	±112	47	±14	18
Lower	784	±55	September 29	539	±180	60	±16	[2] 41
			November 20	549	±214	71	±13	[2] 50
			March 26	357	±95	30	±13	14

[1] This estimate is uncorrected for egg retention. The estimate corrected for egg retention is 82 percent.
[2] These estimates do not differ significantly and are averaged to give 46 percent survival for each date.

measuring the presence of eggs in sampling units at the end of spawning. To measure the presence of eggs, I classified samples with more than three eggs and alevins as points used by spawners and those with fewer eggs as unused. The classification of sample points with three or fewer eggs and alevins as unused is arbitrary, but some small value greater than zero helps correct for the presence of drifted eggs at points not actually used by spawners.

It is probable that the density of eggs in the middle area at the end of spawning was overestimated. The percentage of samples containing more than three eggs and alevins (table 6) did not change significantly for any area from immediately after spawning (September 29) to hatching (November 20). The percentages of samples with more than three eggs or alevins were similar in the upper and middle areas in both September and November, and these similar measures of use in the two areas agree with observed densities of females. Furthermore, the upper and middle areas were similar in terms of the density of eggs and alevins in both November and March (table 5). The potential egg deposition was also about equal in the two areas, and together these observations support strongly the conclusion that density of eggs was overestimated in the middle area at the end of spawning.

Relatively few eggs were unspawned in the body cavities of females. Spawned females retained 5 percent of the potential egg deposition (based on an examination of 173 females).

TABLE 6.—*Percentage of 0.1 m.² sampling units in three areas in Sashin Creek with more than three eggs and alevins, after spawning and during hatching*

Study area	Sampling units with more than three eggs or alevins—			
	After spawning (September 29)		During hatching (November 20)	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
	Percent	*Percent*	*Percent*	*Percent*
Upper	66	±8	68	±9
Middle	73	±7	68	±9
Lower	50	±8	47	±10

Estimates of survival at the end of spawning include allowance for 5 percent retention of eggs by females in the upper and lower areas. In the middle area, however, the density of live and dead eggs at the end of spawning was calculated to be 100 percent of potential egg deposition (equation 3). This estimate is too high and requires further correction for the retention of eggs by females. Because only 95 percent of potential egg deposition was voided during spawning, the estimated 86 percent of live eggs in the middle study area in late September (table 5) pertains to 95 percent (or less) of potential egg deposition. The survival estimate corrected for egg retention is, therefore,

$$0.95 \times 0.86 = 82 \text{ percent.}$$

Correction is also required for two estimates of survival in the lower area where survival was estimated to increase from 41 percent in September to

50 percent in November. Because the difference between 41 and 50 percent survival is not statistically significant, I assume that no mortality occurred in the lower area between September 29 and November 20 and use the average of the two estimates, 46 percent survival, for the spawning period through November 20.

Equation (2) was used to calculate survival in each period. Table 7 gives the results of these calculations.

Instantaneous mortality coefficients corresponding to survival percentages given in table 7 were also calculated. The equation (McNeil, 1966) is:

$$M_{jn}=\frac{-ln(S_{jn})}{t} \qquad (6)$$

where M_{jn} is the mortality coefficient for the jth area and nth period,

S_{jn} is survival for the jth area and nth period, and

t is time.

In computing values of M, the unit of time is taken as 1 month. Thus, $t=1.3$ for period 1; 1.7 for period 2; and 4.2 for period 3. The values of M for each area and period are given in table 8.

TABLE 7.—*Survival of pink salmon of the 1966 brood year in three areas in Sashin Creek*

Study area	Survival from—			Total survival
	Potential egg deposition to actual egg deposition (period 1)	Actual deposition to hatching (period 2)	Hatching to emergence (period 3)	
	Percent	*Percent*	*Percent*	*Percent*
Upper	78	76	39	23
Middle	82	67	33	18
Lower	46	100	30	14

TABLE 8.—*Instantaneous mortality coefficients for pink salmon of the 1965 brood year in three areas in Sashin Creek*

Area	Instantaneous mortality coefficient from—		
	Potential egg deposition to actual egg deposition (period 1)	Actual deposition to hatching (period 2)	Hatching to emergence (period 3)
Upper	0.19	0.16	0.23
Middle	.20	.24	.29
Lower	.60	.00	.30

Changes in the number of live eggs and alevins in each area and in the entire stream are shown in figure 1. The numbers declined in the upper and

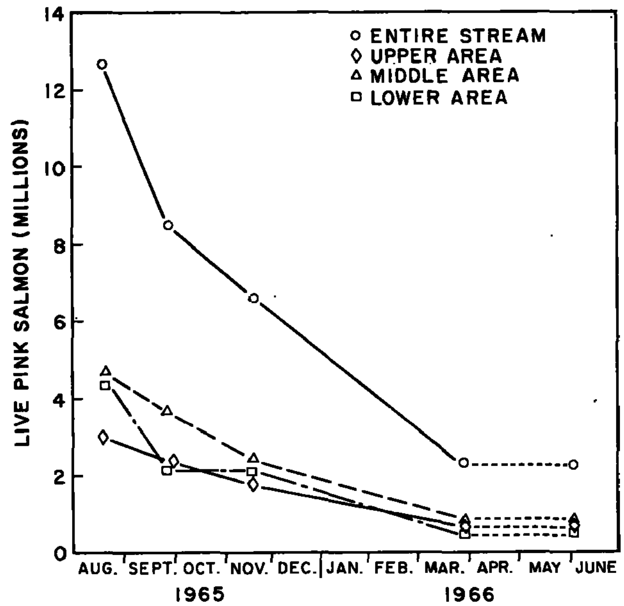

FIGURE 1.—Number of live pink salmon of the 1965 brood year in three areas of Sashin Creek and in the entire stream at beginning and end of four periods in fresh water. The dotted extensions in April and May are for the period of fry migration and are discussed in the text.

middle areas at nearly uniform rates in periods 1, 2, and 3. In the lower area, the numbers declined sharply in periods 1 and 3 but did not decline in period 2. Fry were not counted at the weir in the spring of 1966 because it had been damaged in late winter, but I have assigned 100-percent survival to period 4 (dotted extensions of the curves in figure 1) in all areas on the basis of previous years' data from Sashin Creek (table 9).

Although the density of fry varied among the three areas, the number of fry produced in each was about the same because of differences in sizes

TABLE 9.—*Comparison of estimates of survival of pink salmon fry in Sashin Creek before the fry emerge (hydraulic sampler) and at the time they migrate (weir), 1959–63*

Brood year	Estimates of survival	
	Hydraulic sampler	Weir
	Percent	*Percent*
1959	11.0	13.2
1960	(1)	-----
1961	21.4	20.2
1962	0.0	1.2
1963	20.7	19.6
Mean	13.3	13.6

[1] No estimate.

of the areas. The upper area had the highest number per square meter (228), the middle area the next highest (197), and the lower area the lowest (104).

RELATION OF SURVIVAL OF EGGS AND ALEVINS TO TIME OF SPAWNING OF ADULTS

The observed relation of fresh-water survival to the date by which 50 percent of the spawners entered Sashin Creek is shown in figure 2. The regres-

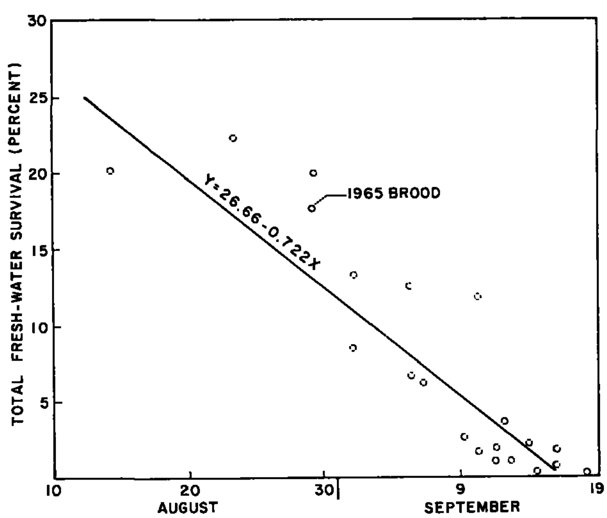

FIGURE 2.—Relation of fresh-water survival of pink salmon in Sashin Creek to date by which 50 percent of spawners entered the stream. The curve $Y=26.66-0.722X$ was fitted by least squares, $X=0$ corresponds to August 10. Relation of the 1965 brood year to the fitted regression is shown.

sion line in the figure is fitted to points for 20 brood years in the period 1940–64. Four years (1952, 1954, 1960, and 1962) were excluded from the regression because potential egg deposition was very meager (12,000 eggs or less) and one year (1964) because the adults were transplanted to the creek.

Fresh-water survival has exceeded that of the 1965 brood year in only three other brood years—1957, 1961, and 1963. In each year 50 percent of the spawners had entered the stream on or before August 26, the "index date" of stream entry for 1965. The date was August 22 in 1957 (22-percent survival); August 13 in 1961 (20-percent survival); and August 26 in 1963 (20-percent survival).

The predicted fresh-water survival of the 1965 brood year based on the regression line in figure 2 was 15 percent. The estimated survival based on the number of alevins collected with a hydraulic sampler (McNeil, 1964a) before the fry emerged from the streambed was 18 percent. An estimated 2,235,-000 fry were produced. Although I could not compare this figure with a count of fry at the weir in the spring of 1966, survival estimated with the hydraulic sampler has agreed closely with survival estimated at the weir (table 9).

It is not entirely clear why fresh-water survival of pink salmon should be high in Sashin Creek when spawners enter early. Merrell (1962) hypothesized that embryos from eggs deposited late in the spawning season fail to develop sufficiently before the onset of cold weather and that embryos of retarded development are more sensitive to adverse effects of cold water than are more developed embryos. High mortality of pink salmon in streams tributary to the White and Barents Seas in 1960 was attributed to late spawning (Azbelev, Surkov, and Yakovenko, 1962).

Laboratory experiments indicate that exposure of salmon eggs to cold water soon after fertilization is detrimental, and this effect may partly explain why late spawning is less successful than early spawning. Eggs of sockeye salmon (*O. nerka*) held at an initial incubation temperature of 7° C. experienced higher mortality than eggs held at 10°, 13°, and 16° C. (Andrew and Geen, 1960), and early exposure of salmon eggs to temperatures of 1° and 2° C. can be lethal (Seymour, 1956; Combs and Burrows, 1957; Efimov, 1962). If incubation temperatures are high enough initially, subsequent reduction to near freezing is not always harmful, but the duration of initial exposure to warm water is important. Seymour (1956) incubated eggs of chinook salmon (*O. tshawytscha*) 2 and 3½ weeks in warm water before exposing them to cold water. He found that eggs reared 2 weeks in warm water had a high mortality when exposed to cold water, whereas eggs reared 3½ weeks in warm water had a low mortality. Additional studies would be required to determine the effect of water temperature on the survival of pink salmon eggs in Sashin Creek and whether warm water during spawning is generally necessary for high survival.

VARIATION AMONG STREAM AREAS IN DENSITY OF FRY

When pink salmon spawners are abundant in Sashin Creek, the entire spawning ground is used intensively; but the largest number of fry per square meter comes usually from the upper area. This fact was discovered first for the 1959 brood fry (Merrell, 1962), and I observed a similar difference in subsequent years when spawners were abundant. The numbers of fry per square meter in the three areas for 4 brood years were as follows (data for the 1959 brood from Merrell, 1962):

Brood year	Lower area	Middle area	Upper area
1959	135	250	325
1961	225	605	600
1963	174	268	360
1965	104	197	228
Mean	160	330	378

Even though the upper area can potentially produce more fry per unit area than the lower or middle area, observations each year since 1958 show that spawners do not concentrate there. In 1965, 14,833 fish (both sexes) spawned at about equal density in the upper and middle areas and at somewhat lower density in the lower area (table 3). In 1964, when the number of spawners was only 2,193, they were concentrated in the lower area, and relatively few were in the upper area (Smedley and McNeil, 1966). In 1963, Sashin Creek had 16,757 spawners, and the number of females per square meter was 50 percent greater in the middle area than in the upper or lower area (McNeil, 1966). Only eight pink salmon spawned in 1962; no observations were made on their distribution. In 1961, 28,759 spawners were distributed fairly uniformly throughout the spawning ground (McNeil, Wells, and Brickell, 1964). Because an attempt was made to destroy the run in 1960, no observations were made on distribution of spawners that year. Data from Merrell (1962) indicated that in 1959, when 35,391 were present, the number of females per square meter in the middle area was at least twice that in the lower or upper. Spawners were scarce in 1958 (217), and they concentrated in the lower area (Merrell, 1962).

The distribution of spawners in Sashin Creek may depend somewhat on the time of spawning. Tagged females in 1963 (table 5 of McNeil, 1966) and 1965 (table 10) "shifted" downstream after the midpoint of spawning: early spawners tended to concentrate in the upper and middle areas and late spawners in the lower area.

TABLE 10.—*Expected and observed numbers of early and late-spawning tagged female pink salmon in three study areas in Sashin Creek, 1965*

[Tagged spawners that first occupied the spawning ground by August 31 were designated as "early"; tagged spawners that occupied the spawning ground September 1 and later were designated as "late"]

Study area	Early spawners		Late spawners	
	Expected	Observed	Expected	Observed
	Number	*Number*	*Number*	*Number*
Upper	25	30	20	15
Middle	36	41	29	24
Lower	41	31	33	43
Total		102		82

χ^2 (2 d.f.) = 9.27 (P, 0.01).

In an earlier paper (McNeil, 1966) I attributed the downstream shift from the upper area in 1963 to turbulent water caused by heavy rainfall in the latter half of the period of spawning (4.5 cm. per day average from September 3 to 29, 1963); but in 1965, rainfall in September averaged less than 0.2 cm. per day, and the streamflow remained low throughout the latter half of the period of spawning—a condition opposite to 1963.

It now appears that late spawners are less inclined to occupy upstream spawning beds of Sashin Creek than are the early spawners, regardless of waterflow. My earlier interpretation of the cause of the downstream shift of the late spawners now appears to be incorrect.

RELATION OF WATER QUALITY TO SURVIVAL AND DEVELOPMENT OF EGGS AND ALEVINS

The concentration of dissolved oxygen in intragravel water in August and September 1965 helped confirm earlier conclusions (McNeil, 1966) that the environment is more favorable for eggs in the upper area than in the middle or lower area. Samples of intragravel water, collected from random points within each area August 16 and 31 and September 13 and 22, were analyzed for dissolved oxygen (table 11).

Dissolved oxygen concentrations of intragravel water were high in August but low in September, when a drought became severe. The low values in September were due partly to consumption of the dissolved oxygen in the stream water by decomposing salmon carcasses. Dead salmon are usually removed from Sashin Creek during freshets, but no freshets occurred in September 1965. The dissolved oxygen cannot be replenished without extensive exposure to the air. The upper area, which has a steep gradient and turbulent water, provided for more rapid replenishment of dissolved oxygen than the calm water in the lower area, which has a shallow gradient. Metabolites that are not freely exchanged with the atmosphere, such as ammoniacal nitrogen, also may have accumulated in the lower area.

TABLE 11.—*Dissolved oxygen content of intragravel water in three areas in Sashin Creek, 1965* [1]

Study area and date	Water temperature	Dissolved oxygen concentration		Degree of saturation
		Mean	90-percent confidence limits of mean	
	° *C.*	*Mg./l.*	*Mg./l.*	*Percent*
Upper:				
August 16	12	9.7	±0.7	90
August 31	12	9.9	± .7	91
September 13	11	6.2	± .9	56
September 22	12	7.6	± .8	71
Middle:				
August 16	12	8.9	± .8	82
August 31	12	9.7	± .7	90
September 13	11	3.8	± .8	34
September 22	12	4.3	± .6	40
Lower:				
August 16	12	8.5	±1.1	78
August 31	[2] 12	-----	-----	-----
September 13	11	2.3	± .3	20
September 22	12	2.9	± .6	27

[1] Methods of sampling were described by McNeil (1962).
[2] The August 31 samples were collected 1 day after a freshet; the data for the lower area are omitted because 60 percent of the standpipes in the area had been washed away.

I expected to find that the percentage of eggs alive at the end of spawning would be highest in the upper area and lowest in the lower area because of the progressively decreasing amounts of dissolved oxygen in intragravel water downstream. On September 29, 84 percent of total eggs were alive in the upper area; 86 percent in the middle area; and 60 percent in the lower area (table 5). Although the lowest survival of eggs was in the lower area, as anticipated, I was surprised to find survival of eggs in the middle area similar to that in the upper area. The percentages of live eggs did not change significantly in any of the areas between September 29 and November 20 (table 5).

The development of embryos was somewhat retarded in the middle and lower areas. Laboratory experiments have demonstrated that oxygen privation during early development may retard growth and development of embryos without causing death (Silver, Warren, and Doudoroff, 1963; Shumway, Warren, and Doudoroff, 1964). When oxygen is deficient, it is usual for hatching to be delayed. This fact was confirmed in Sashin Creek in 1965 where the percentage of eggs hatching by November 20 was 77 percent in the upper area, 30 percent in the middle, and 11 percent in the lower.

The tendency of late spawners to concentrate in the lower area (table 10) may have contributed to the later hatching there, but it was not a factor in the middle area where the proportion of early and late spawners was the same as in the upper area.[2] Temperature apparently was not a factor either, because repeated measurements of the temperature of intragravel water failed to demonstrate differences among the three areas. I conclude, therefore, that hatching was delayed in the middle area because embryos had been exposed to low concentrations of dissolved oxygen in September. The late hatching in the lower area may have resulted from a combination of later time of egg deposition and exposure to low dissolved oxygen.

DISAPPEARANCE OF EGGS AND ALEVINS FROM SPAWNING BEDS

The disappearance of eggs and alevins of the 1965 brood was characterized by (1) disappearance of relatively few eggs from the upper and middle areas in summer during spawning, (2) disappearance of relatively large numbers from the upper and middle areas in autumn after spawning, and (3) disappearance of many eggs from all three areas in winter.

Fewer eggs disappeared during spawning in 1965 than in 1963 even though the densities of spawners were similar (table 12). In 1963, when the density was about 0.6 female per square meter, 22 percent of the potential egg deposition was esti-

[2] A chi-square comparison of the proportion of early and late spawners in the upper and middle areas (χ^2, degree of freedom, =0.17) demonstrated that the proportion of early and late spawners was the same in these two areas.

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mated to have disappeared during spawning in the upper area, 42 percent in the middle area, and 62 percent in the lower area. In 1965, at similar densities of spawners, much smaller percentages of the potential egg deposition disappeared during spawning: 7 percent in the upper area, 5 percent in the middle area, and 31 percent in the lower area.

The high percentage of eggs deposited in 1965 may have resulted from low streamflow in the period of spawning. Except for a freshet on August 30, which produced a discharge of 3 $m.^3$ per second, streamflow remained relatively low (less than 1 $m.^3$ per second) throughout the period of spawning. Streamflow did not increase until October 3 (after spawning had ended) when a second freshet produced a flow of 7 $m.^3$ per second.

TABLE 12.—*Percentage of potential egg deposition of pink salmon that disappeared from three areas in Sashin Creek during autumn and winter, 1963 and 1965 brood years*

Area and season	Estimated portion of potential egg deposition disappearing	
	1963 brood	1965 brood
	Percent	*Percent*
Upper:		
Summer (during spawning)	22	7
Autumn (after spawning)	32	24
Winter	2	27
Middle:		
Summer (during spawning)	[1] 42	5
Autumn (after spawning)	0	26
Winter	1	30
Lower:		
Summer (during spawning)	62	31
Autumn (after spawning)	0	0
Winter	0	24

[1] Estimate pertains to the early two-thirds portion of the period of spawning. Other estimates for summer were at the end of spawning.

A relatively high percentage of the potential egg deposition (36 percent) disappeared from the upper area of Sashin Creek after spawning in autumn 1963, but few eggs and alevins disappeared in winter (table 12). Because the pattern of disappearance was dissimilar in the middle and lower areas in 1963, I postulated that scavengers or predators may have concentrated in the coarse bottom materials of the upper area to feed on eggs and alevins (McNeil, 1966). As I will show shortly, however, turbulent water during periods of high discharge in autumn may also have contributed to the disappearance of eggs from the upper area.

The rate of consumption of eggs and alevins by scavengers and predators is not known, but many species of invertebrates are known to inhabit spawning beds where they may feed on eggs and alevins (Briggs, 1953; Ahnell, 1961; McDonald, 1960). Other investigators (McLarney, 1964, and Phillips and Claire, 1966) have found that sculpins (*Cottus* spp.) are capable of penetrating into streambeds and will feed on eggs and alevins where fine particles do not restrict their movements. The population of sculpins in Sashin Creek has been estimated to include 15,000 to 20,000 fish 5 cm. or longer total length (McLarney, 1964). According to McLarney (personal communication), this number of sculpins would be capable of consuming a significant portion (perhaps 25–50 percent) of the total number of eggs estimated to have disappeared in the autumn of 1963 (about 1 million) and the autumn of 1965 (about 2 million).

McLarney (personal communication) also found that many eggs deposited in coarse materials are near the surface of the streambed and are vulnerable to predation and to removal from the bed by water turbulence. He detected the presence of eggs near the surface of the bed by artificially creating water turbulence within a 0.2-$m.^2$ circular screen placed on the surface of the bed and collecting the eggs that were released from the streambed. About 150 points were tested in this manner in each of the three areas during spawning in 1965 (about 25 points per area on each of six dates). The number of eggs collected by McLarney per 0.2 $m.^2$ in the upper area was 3 times the number in the middle area and 14 times the number in the lower area. Thus, eggs were most susceptible to predation and to removal from the bed by turbulent water in the relatively coarse bed materials of the upper area and least susceptible in the relatively fine materials of the lower area. This result helps to explain why no eggs disappeared from the lower area in the autumns of 1963 and 1965 (table 12).

Other studies have shown that the portion of eggs and alevins that disappear from Sashin Creek spawning beds varies from winter to winter. The number of eggs and alevins did not decrease during the winters 1961–62 and 1963–64 (McNeil et al., 1964; McNeil, 1966); yet in the winter of 1965–66, an estimated 27 percent of potential egg deposition disappeared from spawning beds of Sashin Creek. Factors causing the disappearance of eggs and alevins in the winter of 1965–66 have not been identified.

SEASONAL VARIATION IN MORTALITY IN SPAWNING BEDS

The number of live pink salmon eggs of the 1965 brood declined from an estimated 12.7 million at the beginning of spawning in summer to 8.3 million at the end. Mortality caused further reductions to 6.5 million in autumn and to 2.2 million in winter.

It is instructive to compare mortality of the 1965 brood with that of the 1963 brood. For this comparison, I have calculated values of the mortality coefficient, M, for the entire stream rather than for the individual areas as given in table 8 of this paper and in table 11 of McNeil (1966). The values for M for brood years 1963 and 1965 for period 1 (summer), period 2 (autumn), and period 3 (winter) are as follows:

Brood year	Summer	Autumn	Winter
1963	0.76	0.11	0.07
1965	.31	.15	.26

Although the rate of mortality both years was highest during spawning, the difference between the two years was appreciable (2½ times). Mortality in autumn was similar for the two years, but the difference between the years was pronounced in winter (3½ times). Differences in mortality coefficients are suggestive of differences in the environment encountered by the two populations, because the number of spawners was similar each year (16,757 in 1963 and 14,833 in 1965). The unusual drought which prevailed throughout September 1965 could have produced increased survival during spawning from increased efficiency of egg deposition in spawning beds and decreased survival in autumn and winter from delayed mortality of embryos and alevins exposed to low concentrations of dissolved oxygen early in development.

SUMMARY

1. The area of streambed in Sashin Creek used by pink salmon for spawning is 13,629 m.^{2} Observations on distribution of spawners and survival of embryos and alevins are made annually in 97 percent of the spawning ground which is divided into upper (2,945 m.^{2}), middle (4,067 m.^{2}), and lower (6,072 m.^{2}) areas.

2. Migration of 14,833 pink salmon spawners to Sashin Creek in 1965 was relatively early, and high fresh-water survival of their progeny (18 percent of potential egg deposition) resulted in the production of 2,235,000 fry. High survival was predicted at the time the parents entered the stream from a linear relation of survival of progeny and the date the parents entered the stream.

3. Although the density of spawners was relatively high and fairly uniform throughout the stream, densities of fry were considerably different in the upper, middle, and lower areas. The highest density of fry (228 per square meter) was in the upper area; the lowest (104 per square meter) was in the lower area. The relatively high density of fry in the upper area and low density in the lower area resembled the situation in three previous years (1959, 1961, and 1963) when the density of spawners in the three areas was also relatively high.

4. Spawners do not concentrate in the upper area despite the existence of a favorable environment for embryos and alevins. Failure to concentrate in that area is most pronounced when spawners are scarce, but the reasons for this behavior remain obscure.

5. Delayed hatching of eggs in the autumn of 1965 was attributed to low dissolved oxygen in intragravel water, which resulted from a drought throughout September. Detrimental effects of the drought on embryos were least pronounced in the upper area where concentrations of dissolved oxygen in intragravel water were highest.

6. Rates of disappearance of eggs and alevins from spawning beds in 1965–66 were low during spawning and high during winter in comparison with previous years. Low waterflow in September 1965 may have allowed a better than normal recruitment of eggs to spawning beds. The disappearance of large numbers of eggs and alevins in winter is unexplained.

7. The rate of mortality of the 1965 brood year was two times higher during spawning than in autumn. This situation is contrasted with the 1963 brood, whose rate of mortality was about 7 times higher during spawning than in autumn and about 11 times higher than in winter.

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